



Beta diversity and oligarchic dominance in plant communities of the tropical forests of the Golfo Dulce region, Costa Rica.

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8 **Biotropica**

9 **Editorial Board**

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11 Salamanca, September 5, 2018

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14 Dear Editorial Office,

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16 We are sending you the revised paper ***Beta diversity and oligarchic dominance in***
17 ***plant communities of the tropical forests of the Golfo Dulce region, Costa Rica*** (ID BITR-18-
18 091) prepared as research paper for **Biotropica**. We are very grateful for the work of editors
19 and reviewers, as their suggestions have greatly improved the manuscript.

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21
22 We have carefully checked the English. However, if the article is finally accepted but
23 the quality of the English is not enough, we can pay for language editing by some professional
24 suggested by Biotropica.

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27 Thanks for considering our work for publication in Biotropica.

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31 Best wishes,

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33 Ph.D. Fernando Silla
34 Area of Ecology
35 University of Salamanca
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2 LRH: Morera-Beita *et. al*

3 RHH: Beta diversity and dominance in forests

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6 **Beta diversity and oligarchic dominance in plant communities of the tropical**
7 **forests of the Golfo Dulce region, Costa Rica.**

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28 Received ; revision accepted

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3 29 **B. ABSTRACT PAGE**
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5 30 **ABSTRACT**
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8 31 Recent studies have reported a consistent pattern of strong dominance of a small subset
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10 32 of tree species in Neotropical forests. These species have been called ‘hyperdominant’
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12 33 at large geographical scales and ‘oligarchs’ at regional-landscape scales when being
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14 34 abundant and frequent. Forest community assembly is shaped by environmental factors
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16 35 and stochastic processes, but so far the contribution of oligarchic species to the variation
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18 36 of community composition (i.e. beta diversity) remains poorly known. To that end, we
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20 37 established 20 1-ha plots, i.e. 5 sites with 4 forest types (ridge, slope and ravine primary
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22 38 forest, and secondary forest) per site, in humid lowland tropical forests of southwestern
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24 39 Costa Rica to (1) investigate how community composition responds to differences in
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26 40 topography, successional stage and distance between plots for different groups of
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28 41 species (all, oligarch, common and rare/very rare species) and (2) identify oligarchic
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30 42 species characterizing changes in community composition among forest types. From a
31
32 43 total of 485 species of trees, lianas and palms recorded in this study only 27 species (i.e.
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34 44 6%) were nominated as oligarch species by contributing to 37 % of all recorded
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36 45 individuals with a frequency above 50%. Plant community composition significantly
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38 46 differed among forest types, thus contributing to beta diversity at the landscape-scale.
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40 47 Oligarch species composition was explained by geographical and topographic variables,
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42 48 allowing a confident characterization of the beta diversity among tropical lowland forest
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44 49 stands.
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51 51 **RESUMEN**
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3 52 Estudios recientes han demostrado la existencia un patrón consistente de fuerte
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5 53 dominancia de un pequeño subconjunto de especies arbóreas en los bosques
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7 54 neotropicales. Estas especies han sido llamadas 'hiperdominantes' cuando son muy
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9 55 abundantes y frecuentes a grandes escalas geográficas y 'oligarcas' a escalas de paisaje
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11 56 regional. Aunque tanto los factores ambientales como los procesos estocásticos influyen
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13 57 en el ensamblaje de la comunidad y la diversidad beta, es menos clara la contribución de
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15 58 las especies oligárquicas a la variación de la composición de la comunidad. Con ese fin,
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17 59 establecimos 20 parcelas de 1 ha (5 sitios con 4 tipos de bosque por sitio) en bosques
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19 60 tropicales húmedos de tierras bajas del suroeste de Costa Rica. Los cuatro tipos de
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21 61 bosque fueron: bosque primario de cima, ladera y ripario, y bosque secundario. Los
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23 62 objetivos fueron: (1) Analizar cómo la composición de la comunidad responde a las
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25 63 diferencias en la topografía, la etapa de sucesión y la distancia entre parcelas para los
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27 64 diferentes grupos de especies (todas, oligarcas, especies comunes y raras / muy raras).
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29 65 (2) Identificar las principales especies oligárquicas que mejor caracterizaron los
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31 66 cambios en la composición de la comunidad entre los tipos de bosques. De un total de
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33 67 485 especies de árboles, lianas y palmas registradas en este estudio, solo 27 especies (es
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35 68 decir, 5.94%) fueron consideradas como especies de oligarca al contribuir al 37.41% de
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37 69 todos los individuos registrados y con una frecuencia > 50%. La composición de la
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39 70 comunidad de plantas difirió significativamente entre los tipos de bosques,
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41 71 contribuyendo así a la diversidad beta a escala de paisaje. Las especies oligarcas fueron
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43 72 el mejor componente de la comunidad explicado por variables geográficas y
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45 73 topográficas, permitiendo una caracterización confiable de la diversidad beta a lo largo
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47 74 del paisaje
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77 **C. Key words**

78 Beta diversity, community composition, Neotropical forests, oligarch species,

79 topographic habitats

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3 80 HYPERDOMINANCE HAS RECENTLY EMERGED AS A KEY CONCEPT IN THE STUDY OF
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5 81 TREE DIVERSITY AND FUNCTIONING IN TROPICAL ECOSYSTEMS (ter Steege et al. 2013,
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7 82 Fauset et al. 2015). Ter Steege et al. 2013 defined hyperdominant species as those
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9 83 accounting for half of all individuals inferred at the scale of the tree communities of the
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11 84 Amazon basin. The concept of hyperdominance has its roots in a seminal paper of
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13 85 Pitman et al. (2001), which reported a consistent pattern of dominance by a relatively
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15 86 small but abundant set of tree and palm species, called ‘oligarchs’, in the upland tropical
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17 87 forests of eastern Ecuador and southern Peru. Since then, evidence has accumulated
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19 88 reinforcing the existence of a generalized pattern of oligarchic dominance in tropical
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21 89 forest, especially in the Neotropics (Svenning et al. 2004, Vormisto et al. 2004, Macía
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23 90 and Svenning 2005, Williams et al. 2010, 2017, Macía 2011, Arellano et al. 2014, 2016;
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25 91 see Pitman et al. 2013 for a detailed review). Whereas ‘oligarch’ refers to abundant and
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27 92 frequent species at regional-landscape level, ‘hyperdominant’ defines species very
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29 93 abundant and frequent at large geographical scales (e.g. the Amazon basin). Practical
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31 94 implications of the so-called oligarchic dominance would drastically simplify model
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33 95 parameterization of trophic interactions and critical ecosystem services as water, carbon
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35 96 and nutrient cycling (ter Steege et al. 2013). In fact, Fauset et al. (2015) found that
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37 97 dominance of forest function was even more concentrated in a few species than
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39 98 dominance of tree abundance, with half of the carbon stock and half of woody
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41 99 productivity controlled by only $\approx 1\%$ of hyperdominant tree species throughout the
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43 100 Amazon basin.
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49 101 Whereas studies to date have mainly focused on the effects of oligarch
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51 102 dominance on alpha diversity, less is known of how oligarchic dominance impacts beta
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53 103 diversity. Beta diversity can be defined as the variation in community composition
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55 104 among a set of sites within a given spatial or temporal extent (Whittaker 1960,
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3 105 Anderson et al. 2011). Beta diversity of oligarch communities in tropical forests can be
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5 106 explained by three main hypotheses: (1) Species composition is uniform over large
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7 107 areas, as individuals of all species are able to grow equally well at all sites but
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9 108 differences in abundance are shaped by biological interactions independent of
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11 109 environmental conditions. The best competitors become dominant whereas less good
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13 110 competitors remain rare at all sites (Legendre et al. 2005, Tuomisto and Ruokolainen
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15 111 2006; but see Pitman et al. 2013). As a result, beta diversity will be generally small as
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17 112 the same oligarchic species dominate at landscape level. (2) Species composition
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19 113 fluctuates in a random, autocorrelated way. This hypothesis derives from the neutral
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21 114 diversity model (Hubbell 2001), where individuals of all species are able to grow
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23 115 equally well and all species are competitively equal, but with limited propagule
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25 116 dispersion that spatially structures community composition (Legendre et al. 2005,
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27 117 Tuomisto and Ruokolainen 2006). So, different sets of dominant species will appear at
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29 118 local scales and beta diversity will intrinsically increase with geographical distance.
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31 119 Finally, (3) oligarchies are mainly structured by the same niche mechanisms that
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33 120 generate spatial heterogeneity in tree species composition and abundance (Pitman et al.
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35 121 2013). Oligarch species usually show broader environmental tolerances than less
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37 122 common ones (Brown 1984, Phillips et al 2003, Slatyer et al. 2013, Arellano et al.
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39 123 2014), but they are not necessarily indifferent to environmental heterogeneity, showing
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41 124 higher abundances in the most favorable habitats (ter Steege et al. 2013). In this case,
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43 125 beta diversity will increase with environmental heterogeneity, but this increase is
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45 126 mainly driven by differences in oligarchic abundance and not by turnover in species
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47 127 identity.

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53 128 However, dispersal limitation and niche mechanisms are not mutually exclusive;
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55 129 both structure forest communities and are responsible for patterns of beta diversity

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3 130 across the landscape (Legendre et al. 2009, Cáceres et al. 2012, Qiao et al. 2015). On
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5 131 one hand, propagule limited dispersion and successful recruitment close to conspecifics
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7 132 produce clustered distributions of populations and contribute to community similarity
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9 133 and characterization of oligarch patterns at local scales (Cáceres et al. 2012, Chain-
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11 134 Guadarrama et al. 2012). On the other hand, niche differentiation and environmental
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13 135 gradients e.g. along soil moisture and nutrient availability, slope, and microclimatic
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15 136 factors determine competitive abilities and dominance hierarchies, structuring oligarch
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17 137 communities in space (Sesnie et al. 2009, Cáceres et al. 2012, Pitman et al. 2013,
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19 138 Arellano et al. 2014, 2016, Prada and Stevenson 2016). Whereas most of the studies
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21 139 have shown that both mechanisms contribute to changes in community composition
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23 140 (Condit et al. 2002, Vormisto et al. 2004, Legendre et al. 2009, Baldeck et al. 2012,
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25 141 Cáceres et al. 2012, Chain-Guadarrama et al. 2012, Prada and Stevenson 2016), more
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27 142 work is needed to understand how variation in geographical scale affects the
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29 143 partitioning of beta diversity.
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33 144 We set up our experiment in wet tropical lowland forests in the Golfo Dulce
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35 145 region, southwestern Costa Rica. This region is considered one of the most diverse areas
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37 146 in the country in terms of vascular plants (Zamora et al. 2004, Weissenhofer et al. 2011,
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39 147 Cornejo et al. 2012) and represents the last remaining large tract of lowland rainforest
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41 148 along the Pacific shore of Central America (Gilbert et al. 2016). The complex
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43 149 geological history of the Golfo Dulce region has generated a rich mosaic of landforms
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45 150 (Bagley and Johnson 2014), where forests have been modified by natural and human
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47 151 actions (Weissenhofer and Huber 2001, Gilbert et al. 2016), with $\approx 10\%$ of the Golfo
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49 152 Dulce region covered by secondary regrowth (Weissenhofer et al. 2008). Therefore, we
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51 153 investigated differences in plant community composition across forest types differing in
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53 154 topography and successional stage. Topography is not a direct environmental variable,
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3 155 but a proxy that reflects the variation in soil moisture and microclimatic conditions
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5 156 (Legendre et al. 2009, Cáceres et al. 2009), and thus topographic features are often
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7 157 found to correlate with species distribution patterns (Whittaker 1956, Harms et al.
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9 158 2001). Here, we investigate the following objectives. (1) To analyze how floristic
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11 159 community composition responds to differences in topography, successional stage and
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13 160 spatial distance between plots for the different groups of species. Our hypothesis is that
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15 161 variation within different groups (all, oligarch, common and rare/very rare species) is
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17 162 explained by the same factors than overall species richness, thus oligarchic species
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19 163 represent a subset of the community shaping patterns of beta diversity among tropical
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21 164 tree communities. (2) To identify oligarchic species suitable to characterize shifts in
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23 165 community composition between forest types. As oligarchic are, by definition, frequent
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25 166 in most of the sites, we hypothesized that variation in beta diversity is mostly driven by
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27 167 changes in abundance between forest types for this subset of species.
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34 169 **METHODS**

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37 170 **STUDY AREA.** The study region was located in the Golfo Dulce region, encompassing
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39 171 the Osa Peninsula and the adjacent Piedras Blancas National Park, in Central America,
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41 172 Costa Rica (Fig. 1). Main life zones in the region are tropical wet forests, tropical moist
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43 173 forests and tropical premontane wet forests (Holdridge 1967). Altitude on the Osa
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45 174 Peninsula ranges from sea level to 745 meters asl on Cerro Rincón. The geomorphology
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47 175 in the area is complex, ranging from alluvial sediment plains to rugged uplands
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49 176 produced by tectonic activity with narrow ridges and long steep slopes (Weissenhofer
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51 177 and Huber 2001, Gilbert et al. 2016). The region is dominated by basalt, cherts and
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53 178 limestone lithologies, with inceptisols, ultisols and mollisols as the most abundant soils
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55 179 at the study sites (Alvarado and Mata 2016, Gilbert et al. 2016). Annual precipitation
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3 180 varies between 4000-6000 mm per year. Precipitation shows seasonal variation, with a
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5 181 rainy season from May to December, and four months of reduced precipitation from
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7 182 January to March. Mean annual temperature ranges between 26-27°C (Weissenhofer et
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9 183 al. 2008).

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15 185 PLOT ESTABLISHMENT AND DATA COLLECTION. We selected five sites (La Gamba,
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17 186 Riyito, Agua Buena, Rancho Quemado and Piro) across the study region where in close
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19 187 proximity we could identify each of the four target forest types (Fig. 1). The four forest
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21 188 types were based on physiographic and successional criteria established by previous
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23 189 studies (Clark and Clark 2000, Weissenhofer et al. 2001): ridge primary forest, slope
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25 190 primary forest, ravine primary forest and secondary forest. Ridge plots were established
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27 191 in primary forest growing on the relatively flat and well-drained hilltops (300-400 m
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29 192 altitude), exposed to the action of wind and rain. Slope plots were established in
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31 193 primary forest growing on steep and well-drained slopes. Ravine plots were established
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33 194 in primary forest along streams and adjacent terraces on the bottom of steep slopes.
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36 195 Secondary forest plots were established in previous cleared areas abandoned 25-40
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38 196 years ago according to owners, commonly on moderate to gentle slopes. Secondary
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40 197 forests were situated in accessible topographic positions and had no correspondence in
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42 198 topography with the other forest types. However, secondary forests were included in
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44 199 this study due to their importance in the Golfo Dulce region, where it covers around
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46 200 10% of the landscape (Weissenhofer et al. 2008). In each forest type per location one
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48 201 permanent forest plot was established. Plots were of 1-ha size, and where subdivided in
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50 202 100 subplots of 10x10 m following the standards of Alder and Synnott (1992). Plot
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52 203 shape was adapted to the physiography of the terrain, ranging from regular (100x100 m)
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54 204 to irregular shapes, especially in the case of the ravine where the subplots were situated
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3 205 along the small streams and adjacent terraces. For further information please visit
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5 206 <http://www.univie.ac.at/bdef/php/approach/>.

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8 207 We recorded and tagged all individuals comprising trees, palms and lianas with a
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10 208 diameter at breast height (dbh) ≥ 10 cm, that were mapped in a X- and Y-coordinates
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12 209 system for each plot. Plant samples were collected for taxonomic identification and
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14 210 were deposited at the Herbarium of the University of Costa Rica (USJ). Taxonomic
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16 211 names follow those accepted in the Tropicos data base of the Missouri Botanical Garden
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18 212 (www.tropicos.org).

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21 213 Oligarch species were defined in terms of abundance and frequency (Pitman et
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23 214 2001, Macía and Svenning 2005, Arellano et al. 2014) as the dominant ones that
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25 215 contributed to the accumulated 50 percent of all individuals encountered in all plots
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27 216 together (ter Steege et al. 2013), and were present in at least half (50%) of the plots (≥ 10
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29 217 plots). Excluding oligarch ones, common species were defined with a threshold density
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31 218 ≥ 1 individual/ha (Pitman et al. 2001) and with a frequency ≥ 25 percent of the plots (≥ 5
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33 219 plots). Rare species were defined as those with mean densities < 1 individual per ha
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35 220 and/or frequency less than 25 percent of the plots. Those with only one individual
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37 221 sampled were defined as very rare species.

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44 223 STATISTICAL ANALYSIS. Canonical Analysis of Principal Coordinates (CAP) was used to
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46 224 calculate the centroids of each forest type in the ordination space with all the species
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48 225 (Anderson and Willis 2003). CAP performs a constrained ordination analysis in two
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50 226 steps: (1) Computes a Principal Coordinate Analysis (PCO) of the matrix of the
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52 227 abundance data (which was previously transformed using Hellinger transformation) and
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54 228 using Bray-Curtis as dissimilarity distance (Anderson and Willis 2003, Borcard et al.

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3 229 2018). Use of Bray-Curtis has been debated due to their sensitivity to density invariance
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5 230 (Jost et al. 2011), but we did not identify any significant differences in density within
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7 231 our plots, so we retained using this distance to analyze dissimilarity (Legendre and De
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9 232 Cáceres 2013). (2) Runs a Redundancy Analysis (RDA) of the PCO created above
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11 233 (which act as the response data) constrained by ‘forest type’ as explanatory variable
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13 234 (Anderson and Willis 2003, Oksanen et al. 2017, Borcard et al. 2018). For the CAP
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15 235 analysis, we used the function *capscale* of the *vegan* library under the R environment (R
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17 236 Development Core Team 2013); *capscale* uses all axes with positive eigenvalues, and
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19 237 axes are weighted by corresponding eigenvalues, so that the ordination distances are the
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21 238 best approximations of original dissimilarities (Oksanen et al. 2017, Borcard et al.
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23 239 2018). This implementation makes CAP comparable to Distance-Based Redundancy
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25 240 Analysis (db-RDA; Oksanen et al. 2017, Borcard et al. 2018). Additionally,
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27 241 Permutational Multivariate Analyses of Variance or PERMANOVAs were used to
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29 242 quantify differences in community dissimilarity between forest types (Anderson 2001).
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31 243 PERMANOVA analysis tests the null hypothesis that the centroids of the four forest
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33 244 types, as defined in the space by the abundance of trees, palms and lianas, are equivalent
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35 245 for all forest types (Anderson and Walsh 2013). Thus, if null hypothesis were true, any
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37 246 observed differences among the centroids will be similar in size to what would be
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39 247 obtained under random allocation of individual sample units (plots) to the forest types
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41 248 (Anderson 2001, Anderson and Walsh 2013). A similarity percentage analysis,
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43 249 SIMPER, was used to decompose the Bray-Curtis dissimilarity and to estimate the
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45 250 contribution in percentage of each species to the average overall dissimilarity (Clarke
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47 251 1993). PERMANOVA and SIMPER were performed using the software PRIMER v7
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49 252 (Clarke and Goley 2015).
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3 253 A variation partitioning analysis was performed to examine the contribution of
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5 254 forest types and geographic distance among the plots to community composition
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7 255 (Bocard et al. 1992; Legendre et al. 2009). A redundancy analysis (RDA) was
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9 256 performed to determine the proportion of compositional variation explained by forest
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11 257 types and geographical coordinates. To elucidate the effect of topography among the
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13 258 three primary forests, we repeated the variation partitioning analyses, first including all
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15 259 forest types and second excluding secondary forests. Significance of each fraction was
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17 260 based on 999 random permutations. Variation partitioning was analyzed with the
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19 261 *varpart* library under the R environment (R Development Core Team 2013).

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23 262 To estimate the contribution of the oligarch species on total beta diversity, we
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25 263 used the profile of order q (D_q) (Jost 2006), which is the number of equally-weighted
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27 264 communities, which had no species in common that would yield the observed beta
28
29 265 diversity (Marcon and Hérault 2016). The order q of diversity indicates the sensitivity
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31 266 of the community diversity to common and rare species by modifying how the weighted
32
33 267 mean of the species proportional abundances is calculated (Jost 2006). All values of q
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35 268 less than unity give diversities that disproportionately favor rare species, while all
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37 269 values of q greater than unity disproportionately favor the most common species (Jost
38
39 270 2006, 2007). For $q=1$, all species are weighed by their abundance, without favoring
40
41 271 common or rare species (Jost 2006, 2007). For estimation of the beta diversity profile,
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43 272 we applied the *entropart* library (Marco and Hérault 2016) using the R environment (R
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45 273 Development Core Team 2013).

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49 274 Differences in density and species richness between forest types were tested
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51 275 using one-way ANOVAs with site as block variable after testing for data normality. For
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53 276 ANOVA analyses, we used the *stats* library under the R environment (R Development
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55 277 Core Team 2013).

278

279 **RESULTS**

280 A total of 11,514 live trees were censused and measured. The 86.91 and 96.06 percent
281 of all individuals were identified at the species and genera level, respectively. A
282 significant part of trees (1.66%) identified at genus, but not at species level, belonged to
283 the diversified *Inga* and *Pouteria* genera. We found a total of 485 valid species, 280
284 genera, and 77 families of trees with dbh \geq 10 cm. Mean tree density was 575.65 ± 20.09
285 trees/ha (mean \pm standard error), with no significant differences between sites and forest
286 types. Mean richness was 96.3 ± 6.0 species/ha (mean \pm se), and varied significantly
287 between forest types ($df=3$, $F=13.64$, $p=0.0004$) and sites (blocks; $df=4$, $F=21.72$, $p<$
288 0.0001); with the highest richness in slope and ridge primary forests (110.2 ± 12.0 and
289 103.6 ± 13.6 species/ha, respectively) and the lowest in secondary forests (73.0 ± 9.9
290 species/ha). No significant differences in mean richness were found between primary
291 forests.

292 Considering the 20 plots, only 27 species, i.e. 5.57 percent of all species, were
293 classified as oligarch species. These oligarch species contributed in 37.41 percent of all
294 individuals. 3.7 percent of species are distributed pantropical, 48.1 percent are
295 widespread in tropical America, 33.3 percent are distributed in Mesoamerica and NW of
296 South America, 7.4 percent are restricted to Mesoamerica, and 7.4 percent are endemics
297 of Costa Rica and Panama (Table 1). In the primary forests, a subset of these oligarch
298 species accounted for 31.3-40.6 percent of local abundance, whereas in the secondary
299 forests only 8 oligarch species were locally dominant with 22.0 percent of abundance
300 (Fig. 2). In the sampled sites, the oligarchs with local dominance showed certain
301 variation ranking between 23.6 and 42.8 percent of abundance (Fig. 2). Local dominant
302 species that were not ranked as regional oligarch species contributed to 7.8-26.5 percent

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3 303 and 9.7-28.0 percent of the abundance across sites and forest types, respectively (Fig 2).
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5 304 The most abundant species was the palm *Iriartea deltoidea* (6.97% of all individuals,
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7 305 Table 1 and S2), which was absent at the Piro site, but attained both the highest mean
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9 306 and maximum of abundance (Table 1). The oligarch *Brosimum guianense*, was the
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11 307 unique species that appeared in all the 20 plots. On the other hand, 80.1 percent of the
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13 308 species (392 species) showed a mean density lower than 1 tree/ha and/or a frequency
14
15 309 less than 25 percent, with 98 species only represented by one individual in all the 20
16
17 310 plots (very rare species). These rare and very rare species contributed to ≈ 45 percent of
18
19 311 the total abundance in each forest type (45.9-47.5%; Fig. 2A) or site (41.2-46.9%; Fig
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21 312 2B).

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25 313 The Arecaceae family, with 2 oligarch and 3 common species, was the most
26
27 314 important component of abundance in our study area (11.07% of all individuals),
28
29 315 followed by the Moraceae and the Myristicaceae (Table 2). The Myristicaceae, with 5
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31 316 oligarchs of a total of 8 species was the family with greater proportion of oligarch
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33 317 species. The most diversified family in terms of number of genera and species was the
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35 318 Fabaceae (ranked in the fifth position), showing no oligarch species, but eight common
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37 319 ones.

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41 320 The dissimilarities between the centroids of the four forest types with all species
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43 321 are shown in the CAP graph, where the two first axes explained 82.6 percent of the
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45 322 variation (Figure 3). PERMANOVA test confirmed statistically significant differences
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47 323 between forest types when all species were considered ($df= 16$, Pseudo- $F= 1.8701$, $p=$
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49 324 0.003 , n° of permutations= 998). When pairwise tests with oligarch species were
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51 325 performed, secondary and ridge forest were the most dissimilar, with mean
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53 326 dissimilarities of 49.8 and 47.64% with the other forest types, respectively (Table 3, Fig
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55 327 3). For all the species groups, ridge forest showed significant differences with ravine

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3 328 and secondary forest in community composition. Secondary forest also showed
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5 329 significant differences with slope forest (Table 3). Diversity profile showed that beta
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7 330 diversity increased with order q for oligarch species (Fig. 4). For a diversity of order
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9 331 zero ($q=0$), only absence/presence of oligarchic species is considered, and mean beta
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11 332 diversity was barely apparent among plots. Beta diversity increased as the weight
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13 333 towards the most abundant was higher, and it started to stabilize around $q=2$ (Fig. 4).

16 334 Variation partitioning analysis showed that both spatial distance (geographical
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18 335 coordinates) and forest types explained significant differences in community
19
20 336 composition within forest stands when all, oligarch and common species were selected
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22 337 (Table 4). When all forest types were considered, spatial and forest types had similar
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24 338 weights in explaining community composition (Table 4). However, when only primary
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26 339 forests were considered, spatial distance contributed with most of the explained
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28 340 variation for all species groups, except for oligarch species, where forest type
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30 341 contribution barely changed. Oligarch species was the component of community
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32 342 composition that best responded to spatial and forest type variables, with 42-43% of the
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34 343 explained variation. Overall, the shared explained variation, the environmentally
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36 344 explained variation that is spatially structured, was between 12-16% of the total
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38 345 explained variation (Table 4).

43 346 When oligarch species were used to identify the composition of ridge forests
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45 347 characteristic species were *Componeura excelsa*, *Symphonia globulifera*, *Tapirira*
46
47 348 *guianensis*, *Vochysia ferruginea* and *Pourouma bicolor* (Tables S1 and S2), whereas in
48
49 349 ravine forest *Otoba novogranatensis*, *Chimarrhis parviflora*, *Pleuranthodendron*
50
51 350 *lindenii* and *Tetrathylacium macrophyllum* were the characteristic oligarch tree species
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53 351 (Tables S1 and S2). Although *Iriartea deltoidea* was a common species in all forest
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55 352 types, it showed especially high abundance in the slope forest (Table S2). In fact, slope

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3 353 showed low dissimilarity with both ridge and ravine forests (Fig. 3, Table 2) sharing
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5 354 high abundances of oligarch tree species as *C. excelsa*, *S. globulifera*, *O.*
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7 355 *novogranatensis*, *T. macrophyllum*, *C. parviflora*, and *Sorocea pubivena*, in addition to
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9 356 *I. deltoidea*. On the other hand, secondary forests were characterized by a lower number
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11 357 of oligarch species, such as *Apeiba tibourbou*, *Castilla tunu*, and *Tetrathylacium*
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13 358 *macrophyllum* (Table S1 and S2).
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19 360 **DISCUSSION**

22 361 BETA DIVERSITY AND DIFFERENTIATION OF COMMUNITY COMPOSITION. In tropical
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24 362 forests, changes in diversity of species assemblages across space have been explained
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26 363 by two main mechanisms that spatially structure tree species composition: a) the
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28 364 species-specific response to variation in environmental conditions across gradients or
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30 365 mosaics, and b) the dispersion limitation of propagules over short distances (Harms et
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32 366 al. 2001, Legendre et al. 2005, 2009, Tuomisto and Ruokolainen 2006). Although both
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34 367 mechanisms are not mutually exclusive, their relative contribution varies with spatial
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36 368 extent (Cáceres et al. 2012). At very local scales, neutral processes dominate
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38 369 community composition due to seed dispersal limitation leading to clumped structure of
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40 370 populations, whereas environmental factors linked to topographic and edaphic variation
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42 371 are more relevant with increasing plot size (Legendre et al. 2009, Cáceres et al. 2012).
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44 372 However, at landscape level, some studies have shown that geographical distance is the
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46 373 most important factor explaining composition dissimilarity due to dispersion constrains
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48 374 (Condit et al. 2002, Svenning et al. 2004, Duque et al. 2009, Chain-Guadarrama et al.
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50 375 2012), whereas other studies have shown that this relationship loses significance when
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52 376 environmental factors are included (Sesnie et al 2009, López-Martínez et al. 2013,
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54 377 Prada and Stevenson 2006). Our results show that both spatial distance and
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3 378 environmental variation explain similar amounts of variation among tropical lowland
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5 379 forest types (Table 4). When secondary forests are excluded from analyses, forest type
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7 380 loses importance in explaining the variation in the dataset, highlighting the effect of
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9 381 successional status on forest species composition. However, oligarchic species were not
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11 382 affected by successional status and moreover showed the highest variation explained
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13 383 (42-44% of total variation) in species composition among forest types, in response to
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15 384 both spatial and environmental variables, associated with topography. Topography is
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17 385 considered an indirect environmental variable, summarizing the observed match
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19 386 between species distribution and some environmental variables, as topographic features
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21 387 are correlated with soil drainage, water availability, soil depth and nutrient availability,
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23 388 among others (Legendre et al. 2009, Cáceres et al. 2012). Part of the residual variation
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25 389 is likely explained by environmental variables not assessed by our work, for instance
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27 390 soil variables not related with topography (Chain-Guadarrama et al. 2012, Baldeck et al.
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29 391 2013, Quiao et al. 2015, Prada and Stevenson 2016). Among primary forests, the
30
31 392 greatest difference in community composition was between ridge and ravine forests
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33 393 (Clark et al. 1998, Harms et al. 2001, Weissenhofer et al. 2001, Baldeck et al. 2013,
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35 394 Prada and Stevenson 2016). Slope forests represent a gradual change in community
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37 395 composition from more exposed hill-tops on ridges to the bottom of the stream terraces,
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39 396 and thus showed some similarities in species composition with both ridge and ravine
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41 397 forests.

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46 398 Oligarch species have been reported to have relatively wider niche breadth than
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48 399 common species (Arellano et al. 2014), and in our study were present in most of the
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50 400 plots (64% of oligarchic are present in at least 75% of all the plots), so differences in
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52 401 floristic composition among forest types were mainly attributed to differences in
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54 402 oligarchic abundance, rather than species identity (Figure 4). Wider niche breath does
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3 403 not mean that oligarchic species can be defined as habitat-generalists, conversely many
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5 404 of them can be considered as species with strong preferences for one or two types of
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7 405 habitats where they attain the highest abundances (Clark et al. 1998, Pitman et al. 1999,
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9 406 2013, Legendre et al. 2009, Baldeck et al. 2013, ter Steege et al. 2013, Prada and
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11 407 Stevenson 2016). Only a few oligarch species, like *Brosimum guianense*, *Virola*
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13 408 *koschnyi* or *V. surinamensis*, appeared as generalist species that barely contributed to
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15 409 the differentiation between the forest types (Table S1), and attained regionally high
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17 410 abundances with relatively local low densities in primary forests (Table 1). Conducting
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19 411 taxonomic complete (or almost complete) inventories in tropical forest ecosystems is a
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21 412 highly laborious and arduous task due to technical (climbing to get adequate plant
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23 413 samples) and taxonomic (uncomplete or partial knowledge of the tropical flora)
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25 414 problems (Gentry 1988, Balakrishnan 2005, ter Steege et al. 2013). Oligarchic species
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27 415 are likely less susceptible to misidentification issues due to greater abundance (ter
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29 416 Steege et al. 2013), allowing more confident characterization of beta diversity along
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31 417 environmental gradients (Arellano et al. 2016).
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36 418 All groups of species investigated allowed discrimination of secondary from
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38 419 ridge and slope forests. Gradual change from pioneer to late-successional species is the
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40 420 most obvious explanation of differences in community composition, as secondary
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42 421 forests showed many oligarchic (*Apeiba tibourbou*, *Castilla tunu* and *Cecropia*
43
44 422 *insignis*), common (e.g. *Goethalsia meiantha*, *Hieronyma alchorneoides*, *Alchornea*
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46 423 *costaricensis*) and rare (e.g. *Hampea appendiculate*, *Margaritaria nobilis*) species with
47
48 424 the typical pioneer habit (Clark and Clark 2001, Guariguata et al. 1997, Vandermeer et
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50 425 al. 1997, Wood et al., 2001, Healey and Gara 2003, Peña-Claros 2003, Gilman et al.
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52 426 2016, McClellan et al. 2018). In contrast, secondary and ravine forests showed low
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54 427 dissimilarity in oligarch species composition. Although differences were not strictly
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3 428 significant, common species were better suited to differentiate secondary and ravine
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5 429 forests, due to the high abundance of pioneer species in secondary forest, such as
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7 430 *Alchornea costaricensis*, *Goethalsia meiantha*, *Guatteria chiriquiensis*, *Hieronyma*
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9 431 *alchorneoides* and *Spondias radlkoferi* (Table S1; Lieberman et al. 1985, Vandermeer et
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11 432 al. 1997, Wood et al., 2001, Healey and Gara 2003, Peña-Claros 2003, Gilman et al.
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13 433 2016).

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16 434 Previous studies have shown that low beta diversity characterizes tree
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18 435 communities across habitats in tropical forests, as the most abundant species are usually
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20 436 present in most of habitats (Pitman et al. 2001, Condit et al. 2002, Duque et al. 2003;
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22 437 but see Voormisto et al. 2000). However, as differences between forest types were more
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24 438 linked to variation in abundance and not in composition of oligarch species; changes in
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26 439 beta diversity therefore increased markedly with order of diversity. The diversity of
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28 440 order zero ($q=0$), better known as species richness, is completely insensitive to species
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30 441 abundances as only frequency is considered (Jost 2006, 2007), and changes in
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32 442 community structure were therefore barely apparent among forest types, as oligarchic
33
34 443 species are present in the four forest types. However, focusing on oligarchic species
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36 444 when analyzing species diversity along gradients of increasing species dominances (Jost
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38 445 2006, 2007), such as in hyperdiverse tropical forests, greatly improved to reveal shifts
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40 446 in beta diversity among tropical lowland forest types.

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45 447 CHARACTERIZATION OF FOREST TYPES WITH OLIGARCH SPECIES. Slope and ravine
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47 448 showed the lowest dissimilarity of all the forests, due to the dominance of the two most
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49 449 abundant species that also most contributed to the differentiation from the ridge forest:
50
51 450 *Iriartea deltoidea* and *Otoba novogranatensis*. The palm *I. deltoidea* is also one of the
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53 451 most abundant plant species in the Neotropics (Pitman et al. 2001, Ruokolainen and
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55 452 Vormisto 2000, ter Steege 2013, Arellano et al. 2014). This species is ubiquitous in the

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3 453 sub-canopy domain, found across many soils and forest types (Clark et al. 1995,
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5 454 Ruokolainen and Vormisto 2000), but is negatively affected by flooding in poorly
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7 455 drained habitats (Losos 1995). Although being considered a late successional species
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9 456 (Guariguata et al. 1997), *I. deltoidea* is also found in secondary forests (Losos 1995).
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11 457 Although *I. deltoidea* was common in all our forest types (Table S2), it was especially
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13 458 abundant in the steep slope and ravine plots, as demonstrated in another study in the
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15 459 same region (Huber 2005). Stilt roots in palms such as *I. deltoidea* have shown to allow
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17 460 rapid height growth without loss of stability on steep slopes, allowing the early
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19 461 exploitation of light gaps (Dransfield 1978, Hartshorn 1983, Swaine 1983, Avalos et al.
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21 462 2005), a factor that limits *I. deltoidea* abundance during ontogeny (Svenning 1999). On
22
23 463 the other hand, *O. novogranatensis* is associated to moist but well-drained soils in low
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25 464 altitude locations (Lieberman et al. 1985). Although *O. novogranatensis* is considered a
26
27 465 late successional mid-canopy tree (Cole et al. 2011), it was relatively common in almost
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29 466 all our secondary plots, and it was shown that the large-seeded tree *O. novogranatensis*
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31 467 can be successfully introduced into early stages of succession (Cole et al. 2011).
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36 468 The oligarchs *Compsonaura excelsa* and *Symphonia globulifera*, that are
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38 469 common in both ridge and slope forests with moderate to high densities, exemplify
39
40 470 contrasting life-history traits and biogeographic patterns. *C. excelsa*, a mid-canopy tree
41
42 471 (up to 25 m height in our study sites) with unknown ecology, is an endemic species
43
44 472 restricted to the very humid forests of Costa Rica and west Panamá (Jiménez 2007,
45
46 473 Cornejo et al. 2012). *S. globulifera*, in contrast, has an exceptionally large geographic
47
48 474 distribution from Mexico to Brazil and also presents in tropical West Africa. It shows a
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50 475 plastic ecology, from swampy habitats (Scarano et al. 1997, van Andel 2003) to flat
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52 476 plateaus in well-drained habitats (Hartshorn 1983, Carneiro et al. 2007), which has led
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54 477 some authors to suggest that what is treated as a single species may in fact be at least
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3 478 two species distinguished by morphological and ecological features (Loubry 1994). In
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5 479 our plots *S. globulifera* is a tree of the upper canopy (up to 46 m height), which
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7 480 contrasts with data from other studies where it was usually considered a sub-canopy tree
8
9 481 (Hammel 1986, Gill 1998; but see Hartshorn 1983). Nonetheless, only a few oligarch
10
11 482 species contributed to the differentiation of the community composition of the ridge
12
13 483 plots as *Vochysia ferruginea* and *Pourouma bicolor*. *V. ferruginea* showed high
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15 484 abundance on ridges in other studies in the Golfo Dulce region (Huber 2003), and
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17 485 interestingly was also an abundant species recorded in secondary forests (Guariguata et
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19 486 al. 1997, Letcher and Chazdon 2009; Wood et al. 2011), as was also corroborated by
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21 487 our study. Snapping due to wind exposure and clumps of standing dead trees after
22
23 488 lightning storms are very common disturbances on ridges (Gale 2000, Weissenhofer
24
25 489 2005), likely creating recruitment opportunities for *V. ferruginea*. Hence, studies
26
27 490 reporting fast-growth of saplings after hurricane damage suggest that *V. ferruginea* can
28
29 491 rapidly grow into canopy gaps via a gap-mode of regeneration (Vandermeer et al.
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31 492 1997).

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36 493 Secondary forests showed the lowest species richness, as is common in tropical
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38 494 forests (Guariguata et al. 1997, Peña-Claros 2003), with stem abundance strongly
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40 495 dominated by typical pioneer tree species such as *Goethalsia meiantha*, *Apeiba*
41
42 496 *tibourbou*, *Castilla tunu*, *Hieronyma alchorneoides*, *Alchornea costaricensis*, *Spondias*
43
44 497 *radlkoferi* and *Cecropia insignis* (Vandermeer et al. 1997, Wood et al., 2001, Healey
45
46 498 and Gara 2003, Peña-Claros 2003, Gilman et al. 2016, McClellan et al. 2018), and low
47
48 499 abundance of palm species (Guariguata et al. 1997). Only three species are so frequent
50
51 500 to be considered as oligarch: *Apeiba tibourbou*, *Castilla tunu* and *Cecropia insignis*.
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53 501 These species usually are present in the tree inventories of secondary but also in primary
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55 502 forests (Oliveira-Filho et al. 1998, Clark and Clark 2001, Li et al. 2017), with juvenile

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3 503 stages associated with canopy gaps (Clark and Clark 2001). Only some tree species
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5 504 characteristic of primary forest such as *Tetrathylacium macrophyllum*, *Carapa*
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7 505 *nicaraguensis* and *Otoba novogranatensis* were able to recruit in significant numbers in
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9 506 these secondary forests (Webb 1999, Cole et al. 2011).

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15 508 CONCLUSIONS. Tropical tree and palm species responded to topographic variation
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17 509 among tropical lowland forest stands, thus being characterized by variation in beta
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19 510 diversity across the landscape. Although, secondary forest species composition was
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21 511 reflected by common species, dissimilarity among tropical primary forest types was best
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23 512 captured by differences in oligarch species composition. As many different oligarch
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25 513 species were present in respective forest habitat type, the ability to discriminate
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27 514 differences in community structure improved when the order of diversity increased
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29 515 highlighting the importance of species abundance to classify habitats and explore
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31 516 gradients in beta diversity. The ubiquity of oligarchic patterns in neotropical plant
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33 517 communities has led to the emerging and powerful concept of hyperdominance to study
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35 518 and model important ecosystem functions, such as carbon storage and productivity,
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37 519 nutrient cycling and trophic interactions by focusing on a subset of species (ter Steege et
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39 520 al. 2013, Fauset et al. 2015). Our results corroborate the utility of the hyperdominance
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41 521 concept and extend the concept to the analysis of beta diversity allowing for
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43 522 characterization of hyperdiverse forest communities across tropical landscapes.
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12 531 **DATA AVAILABILITY STATEMENT**

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15 532 The data used in this study are archived at the Dryad Digital Repository (pending
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17 533 acceptance)
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23 535 **LITERATURE CITED**

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789 **TABLE 1.** List of the 20 most abundant palm and tree species in the study region, SW
 790 Costa Rica. Distribution of palms and trees was taken from Cornejo et al (2012) and
 791 www.tropicos.org
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Species	Family	Distribution	% of trees	n° of sites	n° of forest types	n° of plots	Mean density ha ⁻¹ ± se (max. density)
<i>Iriartea deltoidea</i>	Arecaceae	Widespread in Tropical America	6.97	4	4	16	40.15± 8.84 (148)
<i>Otoba novogranatensis</i>	Myristicaceae	Mesoamerica/ NW South America	2.51	5	4	18	14.45± 3.39 (46)
<i>Componeura excelsa</i>	Myristicaceae	Costa Rica/ Panama	2.30	5	4	16	13.25± 3.99 (60)
<i>Tetrathylacium macrophyllum</i>	Salicaceae	Widespread in Tropical America	2.08	5	4	18	12.00± 2.09 (36)
<i>Symphonia globulifera</i>	Clusiaceae	Pantropical	1.97	5	4	18	11.35± 2.01 (24)
<i>Carapa nicaraguensis</i>	Meliaceae	Mesoamerica/ NW South America	1.93	5	4	18	11.10± 2.08 (32)
<i>Tapirira guianensis</i>	Anacardiaceae	Widespread in Tropical America	1.72	5	4	17	9.90± 2.66 (41)
<i>Apeiba tibourbou</i>	Malvaceae	Widespread in Tropical America	1.61	5	4	14	9.25± 3.95 (76)
<i>Castilla tunu</i>	Moraceae	Mesoamerica/ NW South America	1.44	5	4	13	8.30± 4.42 (85)
<i>Perebea hispidula</i>	Moraceae	Mesoamerica	1.22	5	4	19	7.00± 1.40 (24)
<i>Vochysia ferruginea</i>	Vochysiaceae	Widespread in Tropical America	1.02	5	4	11	5.85± 2.43 (39)
<i>Socratea exorrhiza</i>	Arecaceae	Widespread in Tropical America	0.99	5	4	16	5.70± 1.43 (24)
<i>Brosimum guianense</i>	Moraceae	Widespread in Tropical America	0.96	5	4	20	5.55± 0.87 (13)
<i>Tetragastris panamensis</i>	Burseraceae	Widespread in Tropical America	0.92	5	4	14	5.30± 1.86 (31)
<i>Sorocea pubivena</i>	Moraceae	Widespread in Tropical America	0.90	5	4	15	5.20± 1.59 (27)
<i>Brosimum lactescens</i>	Moraceae	Widespread in Tropical America	0.86	5	4	16	4.95± 1.50 (23)
<i>Cecropia insignis</i>	Urticaceae	Mesoamerica/ NW South America	0.86	5	4	14	4.95± 1.64 (29)
<i>Chimarrhis parviflora</i>	Rubiaceae	Costa Rica/ Panama	0.83	5	4	11	4.75± 1.45 (21)
<i>Virola sebifera</i>	Myristicaceae	Widespread in Tropical America	0.82	5	4	14	4.70± 1.93 (33)
<i>Chimarrhis latifolia</i>	Rubiaceae	Mesoamerica	0.80	5	4	11	4.60± 2.93 (45)
<i>Pourouma bicolor</i>	Urticaceae	Widespread in Tropical America	0.80	5	4	11	4.60± 3.23 (51)
<i>Pleuranthodendron lindenii</i>	Salicaceae	Mesoamerica/ NW South America	0.77	5	4	14	4.45± 1.98 (35)
<i>Marila pluricostata</i>	Calophyllaceae	Mesoamerica/ NW South America	0.68	4	4	11	3.90± 1.18 (15)

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3	<i>Viola surinamensis</i>	Myristicaceae	Widespread in Tropical America	0.68	5	4	19	3.90± 0.62 (10)
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5	<i>Lacmellea panamensis</i>	Apocynaceae	Mesoamerica/ NW South America	0.64	5	4	15	3.70± 0.82 (14)
6								
7	<i>Viola koschnyi</i>	Myristicaceae	Mesoamerica/ NW South America	0.58	5	4	18	3.35± 0.57 (9)
8								
9	<i>Vochysia gentryi</i>	Vochysiaceae	Mesoamerica/ NW South America	0.56	4	4	11	3.20± 0.92 (10)
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801 **TABLE 2.** Contribution of the top ten families to the number of trees, percentage of
 802 tree individuals, number of genera and species, as well as number of oligarch and
 803 common species. For reference, we also show the ranking of each family in the Amazon
 804 basin according to ter Steege et al. (2013)

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Family	ter_Steeg et al. (2013) ranking	N° of trees	% of trees	N° of genera	N° of species	N° of oligarch species	N° of common species	
1. Arecaceae	2	1274	11.07	9	9	2	3	
2. Moraceae	8	1004	8.72	12	25	5	7	
3. Myristicaceae	-	822	7.14	3	8	5	1	
4. Malvaceae	5	722	6.27	15	26	1	5	
5. Fabaceae	1	712	6.18	28	57	0	4	
6. Euphorbiaceae	9	532	4.62	10	16	0	4	
7. Clusiaceae	-	481	4.17	6	14	1	5	
8. Salicaceae	-	410	3.56	5	13	2	0	
9. Vochysiaceae	-	408	3.54	2	5	2	2	
10. Meliaceae	-	396	3.44	23	30	30	2	0

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809 **TABLE 3.** Pairwise PERMANOVA tests of dissimilarity between forest types using
 810 oligarch, common and rare and very rare species.

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Species	Groups	t	P(perm)	Unique permutations	Dissimilarity (%)
Oligarch	ridge/ ravine	1.882	0.043	998	48.63
	ridge/ secondary	1.862	0.008	997	55.08
	ridge/ slope	1.336	0.100	997	39.21
	ravine/ secondary	0.930	0.591	999	44.77
	ravine/ slope	1.146	0.227	999	37.67
	secondary/ slope	1.650	0.011	997	49.56
Common	ridge/ ravine	1.599	0.022	999	73.36
	ridge/ secondary	2.156	0.012	999	81.54
	ridge/ slope	0.652	0.903	999	56.05
	ravine/ secondary	1.280	0.090	999	67.80
	ravine/ slope	1.274	0.089	999	67.50
	secondary/ slope	1.928	0.007	998	76.36
Rare and very rare	ridge/ ravine	1.207	0.033	999	89.86
	ridge/ secondary	1.304	0.009	998	94.09
	ridge/ slope	0.846	0.872	998	82.91
	ravine/ secondary	1.061	0.282	999	90.66
	ravine/ slope	1.029	0.343	999	87.70
	secondary/ slope	1.209	0.010	999	93.38

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814 **Table 4.** Variation partitioning analysis of community composition for all the species
 815 groups. Two variables were considered: spatial (geographical position) and forest type.
 816 Shared variation is the amount of explained variation by forest type that is spatially
 817 structured. (a) All forest and (b) only primary forest types (excluding secondary).

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Variation explained (%)	All species	Oligarch	Common	Rare/very rare
(a) All forest types				
Spatial	14.07	19.84	14.32	10.34
F	2.727	3.820	2.780	1.680
<i>p</i> (perm)	0.001	0.003	0.001	0.001
Forest	11.56	15.76	18.45	3.75
F	2.103	2.970	2.464	1.120
<i>p</i> (perm)	0.001	0.001	0.030	0.215
Shared	4.83	7.08	5.64	2.90
Residual	69.54	57.32	61.59	83.01
(b) Only primary forests				
Spatial	16.28	19.15	17.49	13.00
F	2.534	3.820	2.650	1.680
<i>p</i> (perm)	0.001	0.001	0.002	0.003
Forest	5.67	16.15	7.52	1.04
F	1.780	2.940	1.726	1.126
<i>p</i> (perm)	0.017	0.003	0.04	0.195
Shared	4.81	8.33	5.30	2.98
Residual	73.23	56.37	69.68	82.98

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3 822 **FIGURE LEGENDS**
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8 824 **FIGURE 1.** Locations of the five study sites (La Gamba, Riyito, Agua Buena de
9 Rincón, Rancho Quemado and Piro) in in southeastern Costa Rica (Golfo Dulce region).
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11 Rincón, Rancho Quemado and Piro) in in southeastern Costa Rica (Golfo Dulce region).
12 826 In each site, one permanent plot per forest type was positioned.
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18 828 **FIGURE 2.** Proportions of abundance by forest type and site. A) Proportions of stems
19 829 in each forest type belonging to species that are oligarch, local dominant, or neither. B)
20 830 Proportions of stems in each forest type belonging to species that are oligarch, local
21 831 dominant, or neither. Integers show the number of species in each compartment. Local
22 832 dominants (oligarch or not) are species that contributed to the accumulated 50 percent
23 833 of individuals encountered at that forest type or site. Oligarch are species that
24 834 contributed to the accumulated 50 percent of individual in all plots, and at least were
25 835 present in half of the plots.
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39 837 **FIGURE 3.** Canonical Analysis of Principal Coordinates (CAP) showing the distances
40 838 between the centroids of each forest type using the abundance data of all identified
41 839 species. Striped lines of the ellipsoids indicate confidence interval limits at 95% of the
42 840 centroids. Continuous lines of the ellipsoids indicate standard errors of the centroids.
43 841 Dots indicate sampled plots. Site codes: AB (Agua Buena); LG (La Gamba); PR (Piro);
44 842 RQ (Rancho Quemado); RY (Riyito)
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3 844 **FIGURE 4.** Profile of the diversity D_q showing the changes in beta diversity as order q
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5 845 increases using oligarch species. The q order of diversity indicates the sensitivity of the
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7 846 community diversity to common and rare species. For $q=1$, each species is exactly
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9 847 weighted by its proportional abundance All values of q less than unity give diversities
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11 848 that favor rare species, while all values of q greater than unity favor the most common
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13 849 species.

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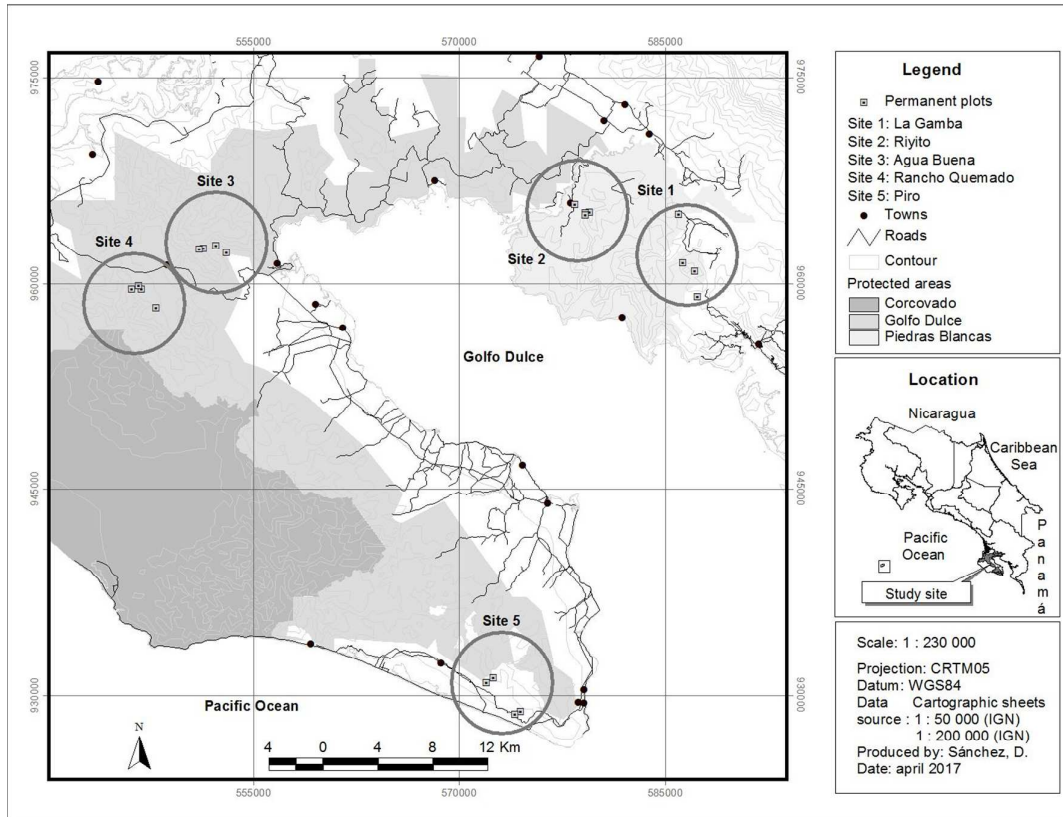
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852 **FIGURES**

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854 **FIGURE 1**

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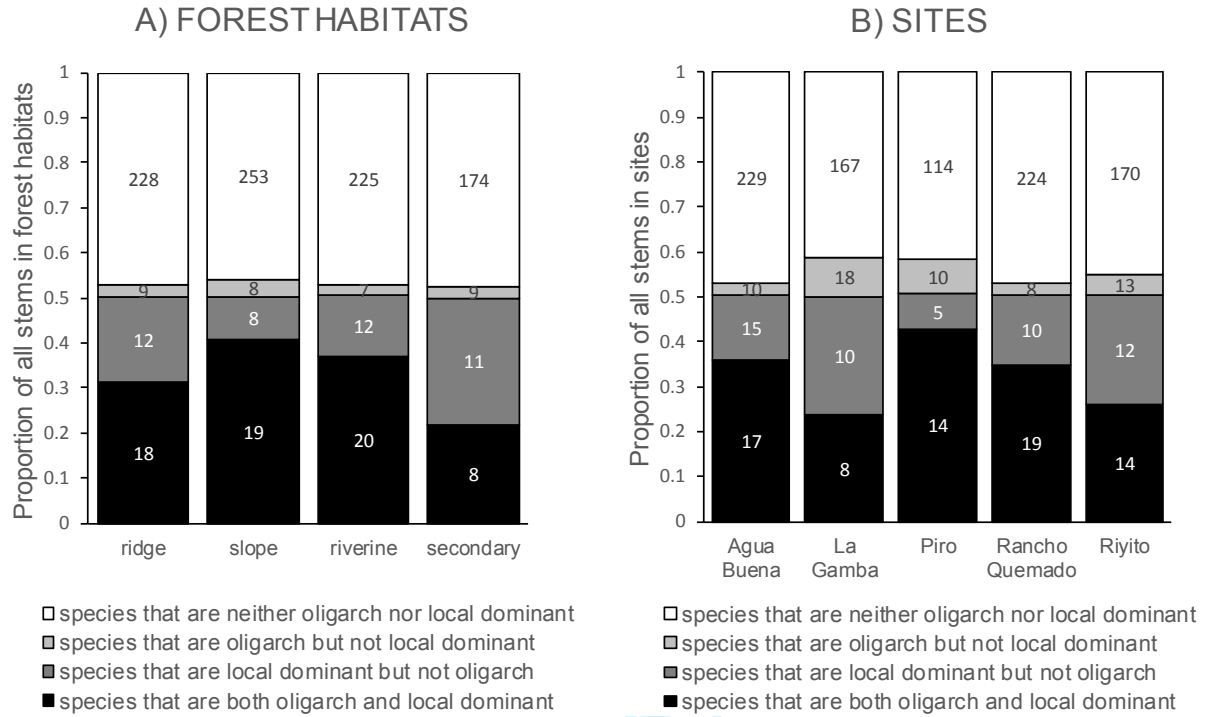
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861 **FIGURE 2**



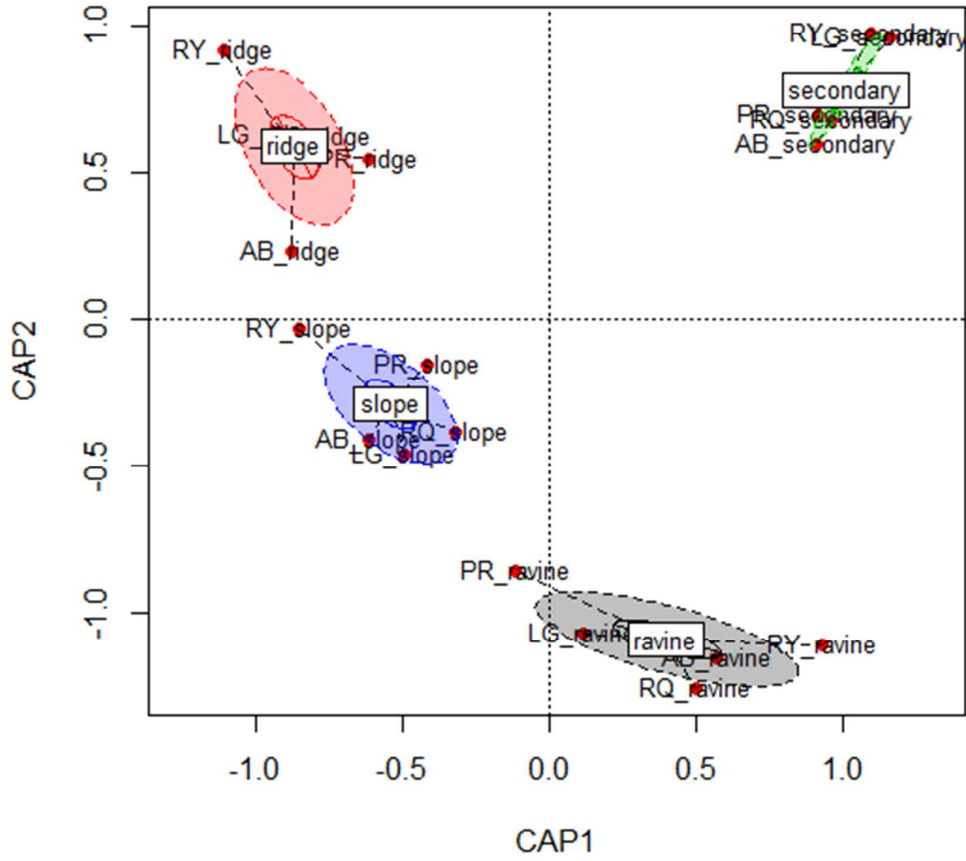
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865 **FIGURE 3**



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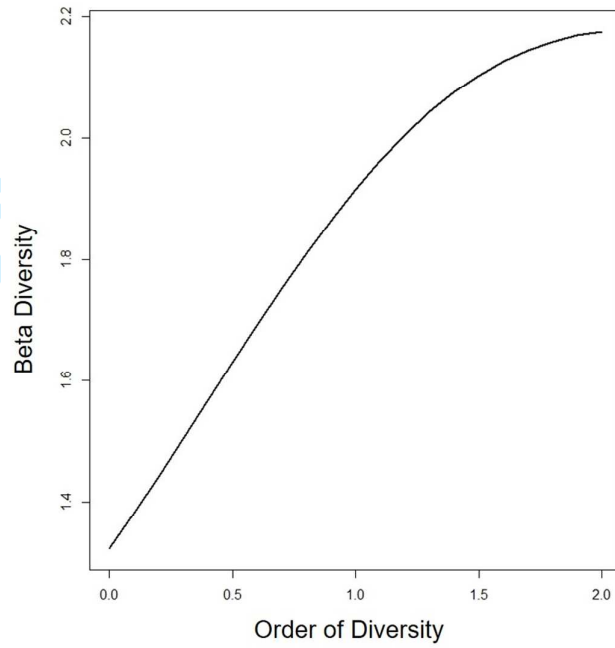
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871 **FIGURE 4**



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879 **SUPPORTING INFORMATION**

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881 **Table S1.** Similarity percentage analyses (SIMPER) between pair of forest types

882 showing the average abundance (Aver.Abund)) and dissimilarity (Aver.Disss) of each

883 species in each forest type. Species where ordered from the species with the highest

884 contribution to the dissimilarity between forest types to the species with the lowest

885 contribution. Diss/SD was calculated as the ratio between average dissimilarity and

886 standard deviation. Contrib% indicates percentage the contribution of each species to

887 the total dissimilarity between forest types.

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Groups Ridge vs Ravine

Average dissimilarity = 48.63

Species	Group RIDGE Aver.Abund	Group RAVINE Aver.Abund	Aver.Disss	Diss/SD	Contrib%	Cum.%
Iri_del	3.49	6.39	3.82	1.5	7.86	7.86
Com_exc	4.48	0.99	3.07	1.55	6.31	14.17
Oto_nov	1.84	4.61	2.8	1.58	5.77	19.94
Voch_fer	2.74	0.57	2.3	1.09	4.72	24.66
Tet_mac	1.29	3.69	2.13	1.8	4.38	29.04
Pou_bic	2.63	0.28	2.12	1.04	4.35	33.39
Ple_lin	0.68	2.31	2.03	1.05	4.17	37.56
Chi_par	0.45	2.66	2.02	2.07	4.16	41.73
Tap_gui	3.5	1.93	1.99	1.66	4.09	45.82
Sor_pub	0.35	2.48	1.91	1.49	3.93	49.75
Sym_glo	4.43	2.51	1.91	1.85	3.92	53.67
Tet_pan	2.33	1.57	1.87	1.21	3.85	57.51
Ape_tib	0.45	2.38	1.82	1.96	3.73	61.25
Bro_lac	2.57	1.54	1.74	1.42	3.57	64.82
Vir_seb	1.88	1.84	1.58	1.34	3.25	68.07
Soc_exo	2.96	2.26	1.55	1.56	3.18	71.25
Car_nic	3.07	2.93	1.54	1.45	3.16	74.41
Cas_tun	0.85	1.38	1.5	1.29	3.09	77.49
Per_his	3.17	2.2	1.38	1.32	2.85	80.34
Mar_plu	1.51	1.46	1.38	1.29	2.83	83.17
Voc_gen	1.84	0.75	1.37	1.3	2.81	85.99
Cec_ins	0.69	1.79	1.36	1.31	2.81	88.8
Lac_pan	2.2	1.37	1.35	1.43	2.78	91.58
Chi_lat	1.2	0.95	1.23	1.1	2.52	94.1

Bro_gui	2.87	1.89	1.12	1.44	2.3	96.4
Vir_kos	1.28	1.98	1.04	1.61	2.13	98.53
Vir_sur	1.73	2.19	0.71	1.36	1.47	100

Groups Rigde vs Secondary

Average dissimilarity = 55.08

Species	Group	Group	Aver.Diss	Diss/SD	Contrib%	Cum.%
	RIDGE	SECONDA RY				
Ape_tib	0.45	4.76	4.25	1.8	7.71	7.71
Com_exc	4.48	0.68	3.69	1.86	6.7	14.42
Sym_glo	4.43	0.89	3.54	3.64	6.42	20.84
Iri_del	3.49	3.3	2.91	1.44	5.28	26.11
Cas_tun	0.85	2.59	2.69	0.93	4.88	30.99
Tet_mac	1.29	3.94	2.67	1.56	4.84	35.83
Voch_fer	2.74	1.77	2.57	1.23	4.67	40.51
Tap_gui	3.5	2.02	2.38	1.48	4.32	44.83
Pou_bic	2.63	0.79	2.16	0.98	3.92	48.76
Car_nic	3.07	2.57	2.08	1.79	3.78	52.53
Soc_exo	2.96	0.98	2.04	1.51	3.7	56.24
Tet_pan	2.33	0.48	2.03	1.17	3.68	59.92
Oto_nov	1.84	2.2	1.98	1.3	3.6	63.52
Lac_pan	2.2	0.4	1.96	1.55	3.56	67.08
Cec_ins	0.69	2.08	1.94	1.07	3.52	70.59
Bro_lac	2.57	0.8	1.77	1.33	3.22	73.81
Voc_gen	1.84	1.12	1.63	1.39	2.96	76.77
Per_his	3.17	1.88	1.62	1.32	2.93	79.7
Mar_plu	1.51	0.2	1.5	1.16	2.71	82.42
Vir_seb	1.88	1.35	1.45	1.53	2.63	85.05
Chi_par	0.45	1.32	1.36	0.85	2.48	87.52
Bro_gui	2.87	1.64	1.36	2.02	2.47	89.99
Ple_lin	0.68	1.51	1.32	1.29	2.39	92.39
Sor_pub	0.35	1.31	1.17	1.45	2.13	94.51
Chi_lat	1.2	0.69	1.11	1.2	2.01	96.53
Vir_kos	1.28	1.83	1.08	1.39	1.95	98.48
Vir_sur	1.73	1.33	0.84	1.3	1.52	100

Groups Ravine vs Secondary

Average dissimilarity = 44.77

Species	Group	Group	Aver.Diss	Diss/SD	Contrib%	Cum.%
	RAVINE	SECONDA RY				
Iri_del	6.39	3.3	4.32	1.81	9.66	9.66
Oto_nov	4.61	2.2	2.99	1.41	6.67	16.33
Ape_tib	2.38	4.76	2.61	1.22	5.83	22.16
Cas_tun	1.38	2.59	2.26	0.83	5.06	27.22
Ple_lin	2.31	1.51	2.16	1.16	4.83	32.05

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3	Chi_par	2.66	1.32	2.16	2	4.83	36.88
4	Tap_gui	1.93	2.02	2.03	1.32	4.52	41.41
5	Cec_ins	1.79	2.08	1.98	1.38	4.41	45.82
6	Vir_seb	1.84	1.35	1.88	1.13	4.19	50.01
7	Soc_exo	2.26	0.98	1.78	1.34	3.97	53.98
8	Voch_fer	0.57	1.77	1.73	0.95	3.87	57.85
9	Sym_glo	2.51	0.89	1.7	1.25	3.8	61.64
10	Car_nic	2.93	2.57	1.56	1.24	3.48	65.13
11	Tet_pan	1.57	0.48	1.4	0.88	3.13	68.26
12	Mar_plu	1.46	0.2	1.37	1.07	3.07	71.33
13	Bro_lac	1.54	0.8	1.34	1.18	2.99	74.32
14	Sor_pub	2.48	1.31	1.33	1.01	2.96	77.28
15	Chi_lat	0.95	0.69	1.26	0.88	2.81	80.09
16	Voc_gen	0.75	1.12	1.26	1.05	2.8	82.89
17	Per_his	2.2	1.88	1.24	1.42	2.76	85.65
18	Tet_mac	3.69	3.94	1.13	1.25	2.53	88.18
19	Lac_pan	1.37	0.4	1.12	1.39	2.5	90.68
20	Vir_sur	2.19	1.33	1.02	1.35	2.27	92.95
21	Com_exc	0.99	0.68	0.86	1.36	1.93	94.88
22	Pou_bic	0.28	0.79	0.85	0.92	1.9	96.78
23	Bro_gui	1.89	1.64	0.79	1.37	1.77	98.54
24	Vir_kos	1.98	1.83	0.65	1.07	1.46	100

Groups Ridge vs Slope

Average dissimilarity = 39.31

Species	Group RIDGE Aver.Abund	Group SLOPE Aver.Abund	Aver.Diss	Diss/SD	Contrib%	Cum.%
Iri_del	3.49	7.58	4.44	1.7	11.32	11.32
Sor_pub	0.35	3	2.17	2.46	5.54	16.86
Oto_nov	1.84	4.11	2.06	1.49	5.25	22.12
Voch_fer	2.74	1	2.05	1.19	5.23	27.34
Tet_mac	1.29	3.56	1.92	1.62	4.9	32.24
Cas_tun	0.85	2.2	1.87	1.19	4.77	37.01
Com_exc	4.48	4.87	1.77	1.5	4.51	41.52
Chi_lat	1.2	2.23	1.76	1.01	4.48	46
Pou_bic	2.63	1.53	1.74	1.1	4.43	50.43
Tap_gui	3.5	2.77	1.56	1.15	3.98	54.41
Car_nic	3.07	3.15	1.48	1.11	3.77	58.18
Mar_plu	1.51	2.28	1.34	1.37	3.43	61.61
Cec_ins	0.69	2.21	1.29	1.63	3.29	64.89
Soc_exo	2.96	1.65	1.26	1.38	3.2	68.1
Chi_par	0.45	1.6	1.23	1.09	3.14	71.23
Voc_gen	1.84	1.29	1.22	1.4	3.12	74.35
Tet_pan	2.33	2.37	1.22	1.26	3.12	77.47
Bro_lac	2.57	2.05	1.19	1.38	3.03	80.5
Per_his	3.17	2.31	1.09	1.38	2.78	83.28
Vir_seb	1.88	1.23	1.05	1.31	2.67	85.95

Lac_pan	2.2	2.24	0.96	1.55	2.45	88.4
Ple_lin	0.68	1.6	0.93	1.55	2.38	90.78
Vir_kos	1.28	1.41	0.87	1.28	2.23	93.01
Bro_gui	2.87	2.39	0.77	1.45	1.96	94.97
Ape_tib	0.45	0.88	0.77	1.2	1.96	96.93
Vir_sur	1.73	2.02	0.66	1.37	1.69	98.62
Sym_glo	4.43	3.99	0.54	1.42	1.38	100

Groups Ravine vs Slope

Average dissimilarity = 37.67

Species	Group	Group	Aver.Diss	Diss/SD	Contrib%	Cum.%
	RAVINE	SLOPE				
	Aver.Abund	Aver.Abund				
Iri_del	3.49	7.58	4.44	1.7	11.32	11.32
Sor_pub	0.35	3	2.17	2.46	5.54	16.86
Oto_nov	1.84	4.11	2.06	1.49	5.25	22.12
Voch_fer	2.74	1	2.05	1.19	5.23	27.34
Tet_mac	1.29	3.56	1.92	1.62	4.9	32.24
Cas_tun	0.85	2.2	1.87	1.19	4.77	37.01
Com_exc	4.48	4.87	1.77	1.5	4.51	41.52
Chi_lat	1.2	2.23	1.76	1.01	4.48	46
Pou_bic	2.63	1.53	1.74	1.1	4.43	50.43
Tap_gui	3.5	2.77	1.56	1.15	3.98	54.41
Car_nic	3.07	3.15	1.48	1.11	3.77	58.18
Mar_plu	1.51	2.28	1.34	1.37	3.43	61.61
Cec_ins	0.69	2.21	1.29	1.63	3.29	64.89
Soc_exo	2.96	1.65	1.26	1.38	3.2	68.1
Chi_par	0.45	1.6	1.23	1.09	3.14	71.23
Voc_gen	1.84	1.29	1.22	1.4	3.12	74.35
Tet_pan	2.33	2.37	1.22	1.26	3.12	77.47
Bro_lac	2.57	2.05	1.19	1.38	3.03	80.5
Per_his	3.17	2.31	1.09	1.38	2.78	83.28
Vir_seb	1.88	1.23	1.05	1.31	2.67	85.95
Lac_pan	2.2	2.24	0.96	1.55	2.45	88.4
Ple_lin	0.68	1.6	0.93	1.55	2.38	90.78
Vir_kos	1.28	1.41	0.87	1.28	2.23	93.01
Bro_gui	2.87	2.39	0.77	1.45	1.96	94.97
Ape_tib	0.45	0.88	0.77	1.2	1.96	96.93
Vir_sur	1.73	2.02	0.66	1.37	1.69	98.62
Sym_glo	4.43	3.99	0.54	1.42	1.38	100

Groups Secondary vs Slope

Average dissimilarity = 49.56

Species	Group	Group	Aver.Diss	Diss/SD	Contrib%	Cum.%
	SECONDA	SLOPE				
	Aver.Abund	Aver.Abund				
Iri_del	3.3	7.58	4.95	1.95	9.99	9.99
Com_exc	0.68	4.87	3.8	2.36	7.66	17.66

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Ape_tib	4.76	0.88	3.43	1.59	6.91	24.57
Sym_glo	0.89	3.99	2.79	2.94	5.64	30.21
Cas_tun	2.59	2.2	2.45	1.02	4.95	35.16
Oto_nov	2.2	4.11	2.37	1.73	4.79	39.95
Tap_gui	2.02	2.77	2.08	1.3	4.2	44.15
Chi_lat	0.69	2.23	1.99	0.94	4.02	48.17
Car_nic	2.57	3.15	1.93	1.96	3.9	52.07
Mar_plu	0.2	2.28	1.93	1.63	3.89	55.96
Tet_pan	0.48	2.37	1.72	2.02	3.47	59.43
Voch_fer	1.77	1	1.67	1.08	3.36	62.79
Lac_pan	0.4	2.24	1.67	2.57	3.36	66.16
Cec_ins	2.08	2.21	1.61	1.58	3.25	69.4
Chi_par	1.32	1.6	1.61	1.19	3.24	72.64
Sor_pub	1.31	3	1.56	1.76	3.14	75.78
Bro_lac	0.8	2.05	1.43	1.6	2.88	78.67
Voc_gen	1.12	1.29	1.29	1.24	2.61	81.28
Vir_seb	1.35	1.23	1.28	1.26	2.58	83.86
Pou_bic	0.79	1.53	1.28	1.15	2.57	86.44
Tet_mac	3.94	3.56	1.24	1.26	2.5	88.93
Soc_exo	0.98	1.65	1.02	1.23	2.05	90.98
Ple_lin	1.51	1.6	0.96	1.46	1.93	92.91
Vir_sur	1.33	2.02	0.9	1.31	1.81	94.72
Per_his	1.88	2.31	0.89	1.17	1.79	96.51
Vir_kos	1.83	1.41	0.87	1.33	1.76	98.27
Bro_gui	1.64	2.39	0.86	1.31	1.73	100

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891 **Table S2.** Top 30 species in each forest type (O: oligarch/ C: common/ R: rare; total
 892 number of individuals)
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Ridge Primary Forest	Slope Primary Forest	Ravine Primary Forest	Secondary Forest
<i>Welfia regia</i> (C; 131)	<i>Iriartea deltoidea</i> (O; 369)	<i>Iriartea deltoidea</i> (O; 258)	<i>Goethalsia meiantha</i> (C; 218)
<i>Compsoeura excelsa</i> (O; 122)	<i>Compsoeura excelsa</i> (O; 130)	<i>Otoba novogranatensis</i> (O; 123)	<i>Apeiba tibourbou</i> (O; 141)
<i>Mabea occidentalis</i> (C; 100)	<i>Otoba novogranatensis</i> (O; 95)	<i>Tetrathylacium macrophyllum</i> (O; 71)	<i>Hieronyma alchorneoides</i> (C; 91)
<i>Symphonia globulifera</i> (O; 99)	<i>Symphonia globulifera</i> (O; 81)	<i>Welfia regia</i> (C; 55)	<i>Castilla tunu</i> (O; 90)
<i>Iriartea deltoidea</i> (O; 95)	<i>Welfia regia</i> (C; 78)	<i>Pleuranthodendron lindenii</i> (O; 51)	<i>Alchornea costaricensis</i> (C; 88)
<i>Qualea paraensis</i> (C; 86)	<i>Tetrathylacium macrophyllum</i> (O; 70)	<i>Carapa nicaraguensis</i> (O; 50)	<i>Tetrathylacium macrophyllum</i> (O; 85)
<i>Tapirira guianensis</i> (O; 72)	<i>Carapa nicaraguensis</i> (O; 64)	<i>Goethalsia meiantha</i> (C; 48)	<i>Iriartea deltoidea</i> (O; 81)
<i>Vochysia ferruginea</i> (O; 64)	<i>Chimarrhis latifolia</i> (O; 58)	<i>Sorocea pubivena</i> (O; 41)	<i>Spondias radlkoferi</i> (C; 81)
<i>Carapa nicaraguensis</i> (O; 62)	<i>Tapirira guianensis</i> (O; 56)	<i>Symphonia globulifera</i> (O; 40)	<i>Gmelina arborea</i> (R; 67)
<i>Pourouma bicolor</i> (O; 61)	<i>Mabea occidentalis</i> (C; 56)	<i>Socratea exorrhiza</i> (O; 40)	<i>Guatteria chiriquiensis</i> (C; 51)
<i>Perebea hispidula</i> (O; 58)	<i>Sorocea pubivena</i> (O; 49)	<i>Chimarrhis parviflora</i> (O; 40)	<i>Carapa nicaraguensis</i> (O; 46)
<i>Marila laxiflora</i> (C; 56)	<i>Qualea paraensis</i> (C; 45)	<i>Virola sebifera</i> (O; 39)	<i>Miconia trinervia</i> (C; 44)
<i>Pausandra trianae</i> (C; 52)	<i>Castilla tunu</i> (O; 43)	<i>Calatola costaricensis</i> (C; 36)	<i>Otoba novogranatensis</i> (O; 43)
<i>Socratea exorrhiza</i> (O; 48)	<i>Marila pluricostata</i> (O; 35)	<i>Eschweilera biflora</i> (C; 35)	<i>Luehea seemannii</i> (C; 43)
<i>Brosimum guianense</i> (O; 44)	<i>Pausandra trianae</i> (C; 33)	<i>Apeiba tibourbou</i> (O; 32)	<i>Cecropia insignis</i> (O; 42)
<i>Tetragastris panamensis</i> (O; 44)	<i>Brosimum guianense</i> (O; 31)	<i>Cleidion castaneifolium</i> (C; 31)	<i>Tapirira guianensis</i> (O; 40)
<i>Brosimum lactescens</i> (O; 41)	<i>Tetragastris panamensis</i> (O; 30)	<i>Tapirira guianensis</i> (O; 30)	<i>Ficus tonduzii</i> (C; 40)
<i>Lacmellea panamensis</i> (O; 33)	<i>Perebea hispidula</i> (O; 29)	<i>Perebea hispidula</i> (O; 30)	<i>Hampea appendiculata</i> (C; 39)
<i>Guarea pterorhachis</i> (C; 32)	<i>Brosimum lactescens</i> (O; 29)	<i>Chrysochlamys glauca</i> (C; 30)	<i>Vochysia ferruginea</i> (O; 36)
<i>Euterpe precatoria</i> (C; 30)	<i>Cecropia insignis</i> (O; 26)	<i>Ocotea rivularis</i> (C; 30)	<i>Platymiscium curuense</i> (C; 31)
<i>Otoba novogranatensis</i> (O; 28)	<i>Lacmellea panamensis</i> (O; 26)	<i>Tetragastris panamensis</i> (O; 29)	<i>Inga oerstediana</i> (C; 30)
<i>Calophyllum brasiliense</i> (C; 28)	<i>Chimarrhis parviflora</i> (O; 25)	<i>Brosimum utile</i> (C; 28)	<i>Jacaranda copaia</i> (C; 28)
<i>Vochysia gentryi</i> (O; 25)	<i>Batocarpus costaricensis</i> (C; 24)	<i>Virola surinamensis</i> (O; 26)	<i>Chimarrhis parviflora</i> (O; 25)
<i>Virola sebifera</i> (O; 21)	<i>Marila laxiflora</i> (C; 23)	<i>Brosimum lactescens</i> (O; 25)	<i>Terminalia amazonia</i> (C; 25)
<i>Marila pluricostata</i> (O; 21)	<i>Virola surinamensis</i> (O; 23)	<i>Cecropia insignis</i> (O; 25)	<i>Trattinnickia aspera</i> (C; 24)

<i>Cassipourea elliptica</i> (C; 21)	<i>Guarea pterorhachis</i> (C; 23)	<i>Peltogyne purpurea</i> (C; 23)	<i>Perebea hispidula</i> (O; 23)
<i>Garcinia madruno</i> (C; 20)	<i>Pourouma bicolor</i> (O; 21)	<i>Cryosophila guagara</i> (C; 23)	<i>Vochysia allenii</i> (C; 23)
<i>Calophyllum longifolium</i> (C; 20)	<i>Protium pecuniosum</i> (C; 20)	<i>Brosimum guianense</i> (O; 21)	<i>Terminalia oblonga</i> (C; 22)
<i>Castilla tunu</i> (O; 18)	<i>Aspidosperma spruceanum</i> (C; 20)	<i>Marila pluricostata</i> (O; 21)	<i>Viola sebifera</i> (O; 19)
<i>Aspidosperma spruceanum</i> (C; 18)	<i>Protium glabrum</i> (C; 19)	<i>Viola koschnyi</i> (O; 21)	<i>Viola koschnyi</i> (O; 19)

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